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2020-02

Wang , Q , Lintunen , A , Zhao , P , Shen , W , Salmon , Y , Chen , X , Ouyang , L , Zhu , L , Ni , G , Sun , D , Rao , X & Holtta , T 2020 , ' Assessing Environmental Control of Sap Flux of Three Tree Species Plantations in Degraded Hilly Lands in South China ' , Forests , vol. 11 , no. 2 , 206 . https://doi.org/10.3390/f11020206

http://hdl.handle.net/10138/313904
https://doi.org/10.3390/f11020206

forests

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Assessing Environmental Control of Sap Flux of Three Tree Species Plantations in Degraded Hilly Lands in South China

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Received: 21 December 2019; Accepted: 4 February 2020; Published: 12 February 2020

Abstract: Prerequisite for selection of appropriate tree species in afforestation programs is to understand their water use strategy. *Acacia mangium* Willd., *Schima wallichii* Choisy, and *Cunninghamia lanceolata* (Lamb.) Hook are the three main vegetation restoration pioneer species in southern China, but no comparative research on the water use strategy of these three tree species have been reported. Our objective was to gain a detailed understanding of how photosynthetically active radiation (PAR), vapor pressure deficit (VPD), and soil water content (SWC) at different soil depths control the sap flux density (J_s) in the dry and wet seasons. We measured the J_s of these three tree species by using the thermal dissipation method in low subtropical China. We found that both *S. wallichii* and *C. lanceolata* differed clearly in their stomatal behavior from one season to another, while *A. mangium* did not. The canopy conductance per sapwood area of *S. wallichii* and *C. lanceolata* was very sensitive to VPD in the dry season, but not in the wet season. The J_s of *A. mangium* was negatively correlated to SWC in all soil layers and during both seasons, while the other two species were not sensitive to SWC in the deeper layers and only positively correlated to SWC in dry season. Our results demonstrate that the three species have distinct water use strategies and may therefore respond differently to changing climate.

Keywords: sap flux density; canopy conductance per sapwood area; dry and wet season; soil water content; *Acacia mangium* Willd.; *Schima wallichii* Choisy; *Cunninghamia lanceolata* (Lamb.) Hook

1. Introduction

China, as the second largest plantation country in the world, has implemented large-scale planned afforestation since the 1950s, primarily focused on planting fast-growing and high production timber species during the 1970s and 1980s [1,2]. These programs have altered the coverage of forest in China from 16.0% in the 1980s to 21.66% in 2018 and this increase is expected to continue as China intends

to extend afforestation for carbon storage and environmental protection [3,4]. Since the 1980s, an extensive afforestation campaign has been conducted in Guangdong Province, and consequently the forest coverage in this region had risen from 26.2% in 1979 to 58.9% in 2016 [5,6]. Although the plantation of pioneer tree species promotes wood yield and increases commercial profits, it consumes a large amount of water [7–9]. However, the use of water by plantations and the selection of appropriate species in many afforestation programs have not previously been considered [10].

Since the 1980s, exotic pioneer species such as *Acacia mangium* Willd, an evergreen broad-leaved tree with nitrogen-fixing, drought-tolerant, and fast-growing characteristics, have been introduced in southern China [11,12]. They can be effectively used due to the nitrogen fixation of the nodule and rapid growth in the early stage to improve soil conditions at the plantations [13]. Observations show that the growth, photosynthetic rate and water use of *A. mangium* plantations decreases after approximately 20–22 years after planting [12]. It can be expected that the use of water is essential to support the growth rate of *A. mangium* [14]. Therefore, understanding the water use strategy of the mature *A. mangium* has been a concern. *Schima wallichii* Choisy is a pioneer, evergreen, broad-leaved and fire-resistant tree species used for timber production and fire protection [15]. It has a wide ecological niche, is particularly common in disturbed and secondary forests [15] and is an important native species for ecological restoration in subtropical southern China. At present, however, there is little research on the water usage of *S. wallichii* in degraded and non-degraded ecosystems. *Cunninghamia lanceolata* (Lamb.) Hook, as an evergreen conifer, is the main traditional pioneer species that has been used for cultivation and wood production due to its rapid growth and excellent wood quality [16]. Moreover, *C. lanceolata* plantations also have positive impacts on ecosystem services, including carbon sequestration [17] and decreasing runoff [18]. According to FAO (2010) [1], in the past four decades, *C. lanceolata* plantations have expanded rapidly and their total planted area has now exceeded 12 million ha in southern China. Despite the positive ecosystem services they provide, there is still a lack of studies on the water use of *C. lanceolata* [19]. Selecting appropriate species and managing forest effectively can optimize the water use in plantations [20,21] as well as potentially maximize economic benefits. However, no comparative research on the water use strategy of these three common vegetation restoration pioneer tree species in southern China has been published.

In South China, human disturbance seriously affected the native evergreen broad-leaved forest, causing soil erosion and leading to vegetation degradation [22]. Since the mid-1980s, a vegetation restoration campaign has been carried out to replace the barren, hilly grasslands with pioneer species including exotic and native species [23]. *A. mangium*, *S. wallichii*, and *C. lanceolata* are the main vegetation restoration tree species, planted in 1985–1990, and they have developed into secondary subtropical forests after more than 30 years under a monsoon climate. These secondary forests are the product of long-term influences of a monsoon climate. Long-term observations have shown that the total annual precipitation has changed little since 1950 in southern China [24]. In recent decades, however, rising air temperature in southern China has shifted the rainfall patterns toward intensified rainfall (i.e., more floods) but has not raised the soil water content (SWC) in the wet season, while droughts are becoming frequent and more severe leading to declining SWC in the extended dry season [24].

In the current study, we set out to find which of these three tree species would be most suitable for planting in the degraded hilly lands in terms of adaptive water-use strategy, especially under the changing climate. In order to answer this question, we should know how the water use of these species is influenced by the environmental factors. We studied the water use of *A. mangium*, *S. wallichii*, and *C. lanceolata* in the degraded hilly lands of southern China using the thermal dissipation technique [25] to measure the xylem sap flux density (J_s) of these species. Our aim is to investigate how photosynthetically active radiation (PAR), vapor pressure deficit (VPD), soil water content (SWC) at different soil depths, and temperature affect J_s of these three tree species in the dry and wet seasons.

2. Materials and Methods

2.1. Site description

The experimental site (112°54′E, 22°41′N) is located in the Heshan National Field Research Station of Forest Ecosystem, Chinese Academy of Sciences, Guangdong Province, China. The average elevation of the station is 80 m. This region is dominated by a subtropical monsoon climate, with an annual average precipitation of 1700 mm, and temperature of 21.7 °C. The annual accumulated temperature above 10 °C is 7600 °C, and the annual solar radiation is 4350 MJ m^{-2}. There are distinct wet and dry seasons in this region. The wet season lasts approximately from April to September, while the dry season is approximately from October to March [26].

Our experiment was conducted in the three mono-species plantations of *A. mangium*, *S. wallichii*, and *C. lanceolata* (Table 1) from January to December in 2017. These three plantations were planted between 1985 and1990, located close to each other on different hill slopes with similar elevation (80 m), inclination, slope (20%–30%) direction, and soil properties (Table 2). We randomly selected 15 trees of each tree species for the sap flow experiment (Table 3).

Table 1. Site characteristics of three sites.

Site	Plot Size (m^2)	Tree Density (No. ha^{-1})	Total Stand Basal Area (m^2 ha^{-1})	Mean DBH ± Standard Error (cm)	Mean Height ± Standard Error (m)
A. mangium	1600	519	26.2	23.5 ± 1.1	14.5 ± 0.5
S. wallichii	900	867	31.0	20.2 ± 0.8	12.2 ± 0.5
C. lanceolata	800	725	11.1	11.8 ± 1.0	9.5 ± 0.6

DBH, diameter at breast height (1.3m).

Table 2. Physical properties, water holding capacity, and storage performance of three plantation soils.

Site	Soil Bulk Density ($g{\cdot}cm^{-3}$)	Maximum Water-Holding Capacity ($g{\cdot}kg^{-1}$)	Field Capacity (%)	Non-Capillary Porosity (%)	Capillary Porosity (%)	Total Porosity (%)
A. mangium	1.3 ± 0.04	327.0 ± 17.2	25.6 ± 0.9	8.6 ± 1.1	33.9 ± 1.0	42.5 ± 0.8
S. wallichii	1.4 ± 0.04	296.3 ± 17.3	24.4 ± 1.2	7.0 ± 0.6	33.5 ± 0.8	40.5 ± 1.0
C. lanceolata	1.4 ± 0.04	290.8 ± 14.6	23.4 ± 0.7	7.6 ± 1.2	32.5 ± 0.7	40.1 ± 0.8

Table 3. DBH, tree height and mean daily maximum sap flux density (J_{smax} ± standard error) of the three species.

Species	*A. mangium*			*S. wallichii*			*C. lanceolata*		
Tree No.	DBH (cm)	Height (m)	Mean Daily J_{smax} ($g\ m^{-2}\ s^{-1}$)	DBH (cm)	Height (m)	Mean Daily J_{smax} ($g\ m^{-2}\ s^{-1}$)	DBH (cm)	Height (m)	Mean Daily J_{smax} ($g\ m^{-2}\ s^{-1}$)
1	27.6	16.3	34.4 ± 1.0	22.9	14	18.7 ± 0.7	17.5	13.5	3.8 ± 0.1
2	16	14.9	14.2 ± 1.1	23.3	13	18.7 ± 0.7	24.2	13.8	18.2 ± 0.6
3	40.3	17.8	56.7 ± 1.2	20.1	13	25.2 ± 1.3	22	13.5	5.7 ± 0.2
4	23.6	17.5	8.8 ± 0.4	16.4	10.6	19.2 ± 0.7	19	13	5.3 ± 0.2
5	27.3	17	24.4 ± 1.1	19	12.3	19.1 ± 0.7	14.3	11	6.2 ± 0.2
6	17.4	15.6	17.2 ± 0.6	30.3	15.5	38.5 ± 1.4	18.6	13.13	8.2 ± 0.3
7	33.9	17	39.2 ± 1.1	13.1	11	13.7 ± 0.7	18.1	13	12.4 ± 0.4
8	19.8	11	30.8 ± 0.8	16.6	12	10.7 ± 0.5	10.5	10.6	3.0 ± 0.1
9	29.2	17	54.9 ± 1.3	16.1	11	24.2 ± 0.9	21.2	11.5	7.9 ± 0.3
10	32.1	16.2	28.2 ± 1.4	19.3	14	32.4 ± 1.0	16.5	10.5	6.4 ± 0.2
11	40	17.5	43.6 ± 1.5	18.4	11.5	13.8 ± 0.5	22	13	4.0 ± 0.1
12	28.6	16.5	16.3 ± 0.9	21.1	13	26.4 ± 1.0	11.2	10.5	13.5 ± 1.2
13	34.8	15	38.1 ± 1.1	32.2	17	29.4 ± 0.9	18.3	11.1	9.1 ± 0.3
14	27.5	11	10.2 ± 0.6	18.2	12.5	29.3 ± 1.0	13.7	11.5	3.4 ± 0.1
15	30.5	15.2	24.0 ± 1.1	17.4	12.3	21.2 ± 1.0	19	13	9.5 ± 0.4

2.2. Measurements

2.2.1. Microclimate

PAR, temperature, relative humidity (above 2 m), and wind speed data (above 10m) were measured (VAISALA MAWS301, Vaisala, Espoo, Finland) and data was provided by the Heshan National Field

Research Station of Forest Ecosystem. The leaf area index (LAI) was measured by LAI 2000 (LI-COR, Lincoln, NE, USA) monthly. The linear distances from the station to the *A. mangium*, *S. wallichii*, and *C. lanceolata* sites were 300, 50 and 100 m, respectively. Hourly averages were used for all meteorological data and we calculated VPD (kPa) according to Campbell and Norman, 1998 [27]:

$$VPD = a \times exp\left(b \times \frac{T}{T+c}\right)(1 - RH) \quad (1)$$

where a, b, and c are constant parameters i.e., 0.611 kPa, 17.502 (unitless), and 240.97 °C, respectively, and RH is relative humidity (Units), T is temperature (Units).

2.2.2. Soil Water Content

The soil type at all the sites is lateritic red soil. The soil water content (SWC) was measured at 5, 10, 20, 30, 40, 50, 60, 90, 120, and 150 depths at three locations (up-, mid-, and downslope) at each site using soil moisture sensors (A755 GPRS, Adcon, Klosterneuburg, Austria). An Adcon A755 telemetry unit (Adcon) transmitted the data signals to a data server at 30 min intervals.

2.2.3. Sap Flow

We used home-made Granier's sensors (thermal dissipation probes, TDPs) to measure sap flow of 15 sample trees in each of the three plantations [25]. The TDP sensors consisted of a pair of 20-mm-long and 2 mm in diameter stainless steel probes. Each pair of probes was inserted on the northern side of the stem (1.3 m above ground) approximately 10 cm apart along the axis of the hydro-active xylem. The upper probe was heated by a DC supply of 120 mA, yielding a constant power of 0.2 W, while the lower probe remained unheated. We converted the instantaneous temperature difference between the two probes into a voltage value recorded by a data logger (Delta-T logger DL2e, Delta-T Devices Ltd., Cambridge, UK). The data were measured every 30 s and stored as 10 min averages [14]. Finally, we calculated J_s (g $m^{-2}s^{-1}$) following Granier (1987) [25]:

$$J_s = 119 \times \left(\frac{\Delta T_{m-}\Delta T}{\Delta T}\right)^{1.231} \quad (2)$$

where ΔT_m is the temperature difference between the two probes obtained under zero flux conditions and ΔT is the instantaneous temperature difference. The "zero baseline" was determined on nights when VPD was zero or nearly zero for several hours, so that there was no driving force for sap flux. ΔT_m was determined separately for each tree over 7 days to avoid the underestimation of nocturnal sap flow [28]. The voltage value data was converted to J_s by applying the Baseliner 4.0 program [29] (https://github.com/Coweeta/Baseliner4_exe).

2.2.4. Canopy Conductance per Sapwood Area

Because of the difficulty in obtaining the leaf area data of measured trees, canopy conductance per sapwood area (g, mmol m^{-2} s^{-1}) was determined by using the following formula:

$$g = \frac{J_s}{VPD} \quad (3)$$

which presumes that J_s is equal to canopy transpiration, and J_s is not influenced by hydraulic capacitance [30,31].

2.3. Data Analysis and Modeling

We analyzed both the daily and hourly relationships between the environmental conditions and J_s since the daily analysis fails to catch fast responses to changing environmental conditions, while the hourly analysis in obscured by time lags. We concentrated more on the analysis of the daily data by

looking at daily average values (which need not to occur at the same moment in time) to minimize the problems caused by the time lag due to the internal water stores, i.e., capacitance [32], and due to the slowness of the thermal dissipation probe method to respond to changes in flow rate [33,34]. We first used the daily average values of J_s, PAR, VPD, and SWC, then after correcting the time lag between VPD, PAR and J_s, we used the hourly average values minus the daily average values of J_s, PAR, and VPD to analyze the hourly dynamics of J_s within a day. We analyzed the relationship between the dependent variable J_s and the explanatory variables PAR, VPD, and SWC in the daily and hourly (only PAR and VPD) tree-level data:

$$\ln(J_s) = \ln(\alpha) + \beta 1 \times \ln(PAR) + \beta 2 \times \ln(VPD) + \beta 3 \times \ln(SWC) \quad (4)$$

The parameters β1, β2, and β3 describe the sensitivity of J_s to the natural logarithm (better fit than other shapes) of PAR, VPD, and SWC, respectively (note that this is equivalent to fitting a power function $J_s = \alpha\,(PAR)^{\beta 1}(VPD)^{\beta 2}(SWC)^{\beta 3}$). All the statistical analyses were produced by R software (R Core Team; R version 3.5.3; RStudio version 1.1.463). The analysis for hourly data was made separately (1) for each species during the wet and dry seasons, (2) for small and large trees of each species, and (3) for each species with SWC measured at different soil depths. The size class in (2) was determined based on DBH separately for each species (note that in (1) and (2) the data were divided into two approximately similar size groups). The random term tree identity was added into the models to consider the dependence of observations for the same tree, and all values were transformed for the statistical analysis with natural logarithm. Possible differences in the relationship between J_s and the explanatory variables VPD, PAR, and SWC between species, between wet and dry seasons, between small and large trees, and between models with SWC measured at different soil depths were compared with 95% confidence intervals (Tables 4–6); for example, if the confidence interval of the estimate of the effect of VPD on J_s in the wet season overlapped with the estimate of the effect of VPD on J_s in the dry season in *A. mangium*, no significant difference was reported. Temperature was left out of the model because temperature is highly correlated with another variable in the model, VPD. However, we compared the residuals of the model with temperature to test whether temperature had a direct (i.e., not through VPD) effect on sap flow. The effect of wind speed on J_s was also analyzed, but it was not significant and was thus dropped from the final analyses.

3. Results

3.1. Micrometeorology

The total amount of precipitation recorded was 1673 mm from January 2017 to December 2017, which was in the range of the long-term annual mean in the Heshan area. Rainfall in the wet season (1289 mm) accounted for 77% of the total annual precipitation (Figure 1a). The mean daily PAR was 223 (±9) μmol $m^{-2}s^{-1}$ and 326 (±13) μmol $m^{-2}s^{-1}$ during the dry and wet periods, respectively (Figure 1c). The mean daily VPD was 0.55 (±0.03) kPa and 0.59 (±0.03) kPa in the dry and wet season, respectively (Figure 1d). The average daily temperature ranged from 8.7 to 31.8 °C during the whole measurement period (Figure 1f). The mean daily PAR, VPD, and temperature were all higher in the wet season than in the dry season. The difference in mean SWC of all layers between the wet and dry seasons was greater at the *A. mangium* and *S. wallichii* sites than at the *C. lanceolata* site (Figure 2). At the *A. mangium* site, average SWC of all layers was lower in the dry season (19%–28%) compared with the wet season (28%–33%) (Figure 2). At the *S. wallichii* site, average SWC of all layers ranged from 20% to 27% in the dry season and from 26% to 32% in the wet season, which can be compared with the average SWC of all layers of 20% to 26% in the dry period and 25% to 30% in the wet period at the *C. lanceolata* site (Figure 2). The leaf area index (LAI) of all the three sites decreased in the dry season compared with the wet season, and the decrease at the *A. mangium* site was larger (25%) than at the *S. wallichii* (18%) and *C. lanceolata* sites (10%) (Figure 1b).

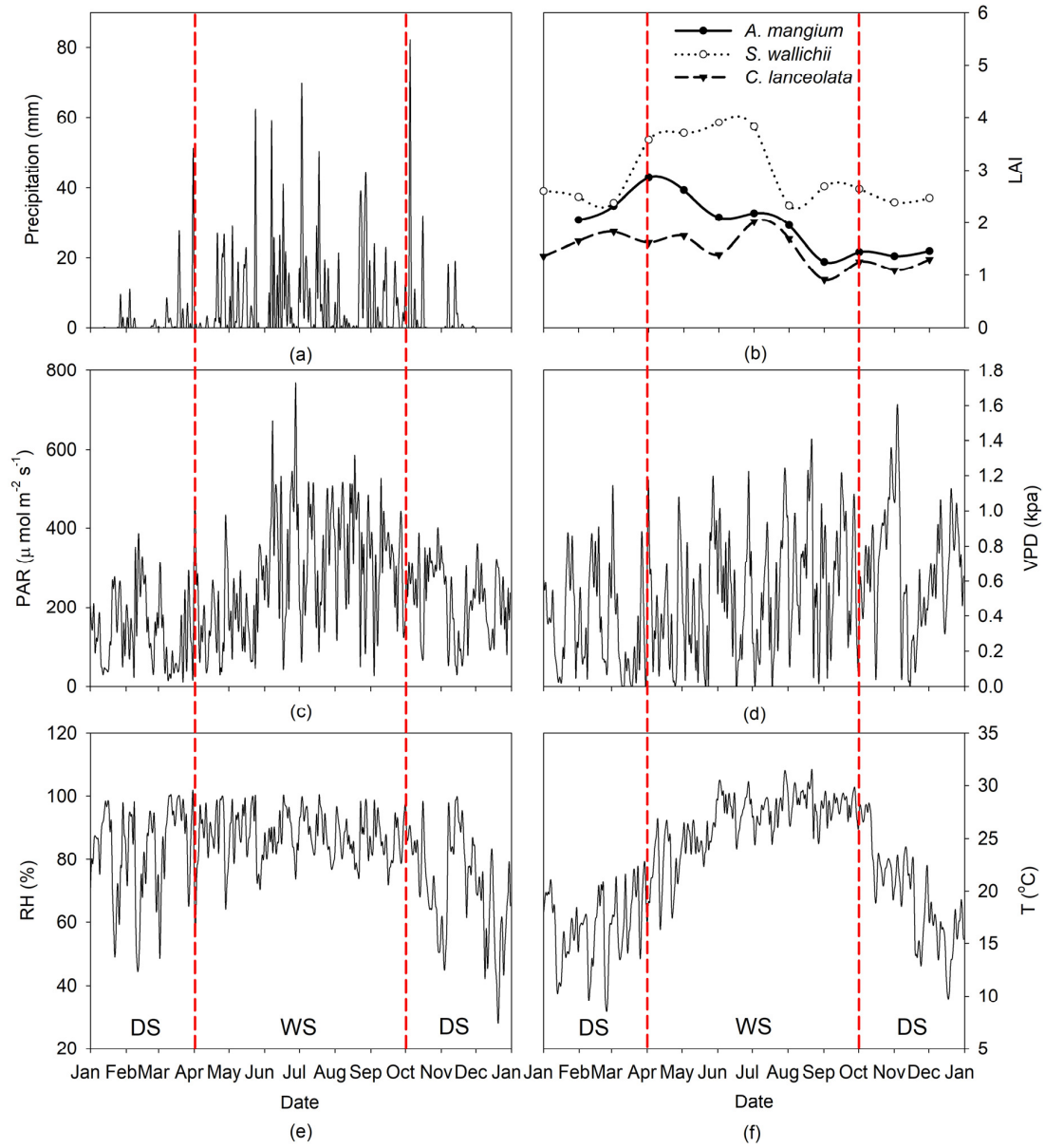

Figure 1. (**a**) Daily precipitation, (**b**) monthly leaf area index (LAI), daily mean values of (**c**) photosynthetically active radiation (PAR), (**d**) vapor pressure deficit (VPD), (**e**) relative humidity (RH) and (**f**) temperature (*T*) during dry season (DS) and wet season (WS) in 2017.

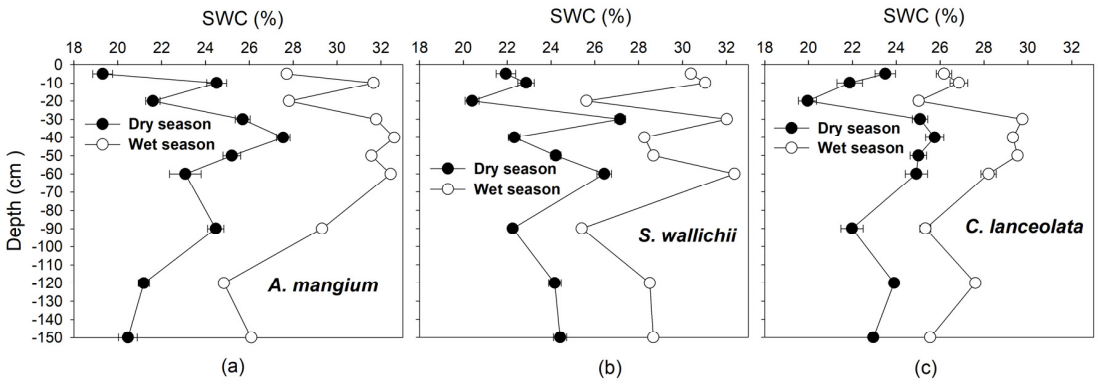

Figure 2. Soil water content (SWC± standard error) at 10 different depths in the dry and wet seasons at three sites. (**a**) *A. mangium* site; (**b**) *S. wallichii* site; (**c**) *C. lanceolata* site.

3.2. Sap Flow Density and Environmental Effects

The recorded mean daily maximum J_s was in the range of 8.8 (±0.4) to 54.9 (±1.3) $gm^{-2}s^{-1}$ (DBH range = 16–40 cm) for the *A. mangium*, 10.7 (±0.5) to 38.5 (±1.4) g $m^{-2}s^{-1}$ (DBH range = 13–32 cm) for the *S. wallichii*, and 3.0 (±0.1) to 18.2 (±0.6) g $m^{-2}s^{-1}$ (DBH range = 11–24 cm) for the *C. lanceolata* (Table 3). The mean J_s of *A. mangium* and *S. wallichii* was two times larger than that of *C. lanceolata* in magnitude (Figure 3). At these three sites, the highest J_s occurred between April and October during the wet season, coinciding with the highest *T* and PAR measured during the year. The lowest values were recorded between December and March during the dry season. The J_s was similar between the dry and wet seasons for *A. mangium*, while J_s was different between the dry and wet seasons for *S. wallichii* and *C. lanceolata* (Figure 3).

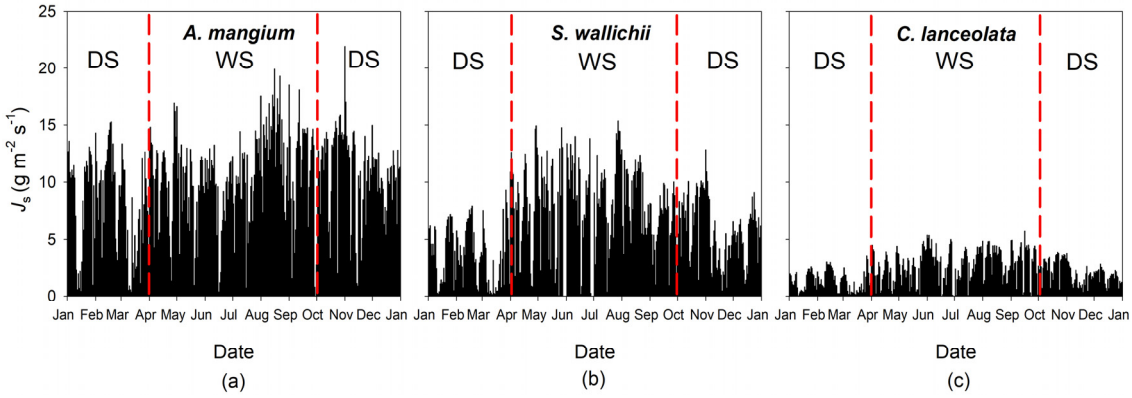

Figure 3. Daily mean J_s averaged for all the sap flow-monitored trees in each plot during dry season (DS) and wet season (WS). (**a**) *A. mangium* site; (**b**) *S. wallichii* site; (**c**) *C. lanceolata* site.

We compared the analysis results regarding sensitivity of J_s to environmental variables separately during the wet and dry seasons and in small and large trees. No significant difference in the correlation coefficient of J_s with PAR or VPD between small and large trees of any species was found, and therefore, the results are not shown. Figure 4 demonstrates raw data (i.e., without using the statistical model) of J_s and single environmental drivers during the wet and dry seasons. Tables 4–6 show results from the mixed models that consider the effect of all the environmental drivers simultaneously, thus showing the actual dependencies between the studied variables when the effects of all environmental drivers are considered in the model. Table 4 shows the results for the daily average values (abbreviation daily data) for all the variables and Table 5 shows the hourly average values minus daily average values (abbreviation hourly data) for all the variables. Note that to obtain the response of canopy conductance per sapwood area to the environmental factors, 1 should be subtracted from coefficient β2 (compare Equation (3) and Tables 4 and 5), while coefficients β1 and β3 for the canopy conductance per sapwood area are the same as for J_s.

The J_s of *A. mangium* was affected on the daily scale by PAR, VPD, and SWC in both seasons, and it was more sensitive to PAR in the dry season than in the wet season (Table 4). SWC affected J_s negatively during both seasons and in all soil layers (Tables 4 and 6). On the daily scale, J_s of *S. wallichii* was sensitive to VPD but the parameter β2 was nearly zero in dry season (Table 4). Note that this indicates strict canopy stomatal control as stomata closure occurs concurrently with increases in VPD, while transpiration (J_s used as a proxy) remains unchanged (Equation (3)). Moreover, J_s of *S. wallichii* was significantly correlated with SWC in the two topmost soil layers, SWC1 and SWC2 (Table 6), and the sensitivity of J_s to SWC was significant only during the dry season (Table 4). On the daily scale, J_s of *C. lanceolata* was strongly related to PAR and SWC but not affected by VPD in the dry season; in the wet season, it was positively affected by PAR and VPD (Table 4). The J_s of *C. lanceolata* showed no sensitivity to VPD and the parameter β2 was nearly zero, also indicating that its canopy conductance per sapwood area was very sensitive to VPD. Only SWC in the topmost soil layer (SWC1) significantly

affected the J_s (Table 6). J_s of *S. wallichii* and *C. lanceolata* was more sensitive to PAR but less sensitive to VPD in dry season than in wet season (Table 4). There were distinct differences among these three species in their sensitivity to the environmental factors. The J_s of *A. mangium* was less sensitive to PAR and SWC but more sensitive to VPD than that of the other two species in the dry season, but less sensitive to VPD in the wet season (Table 4).

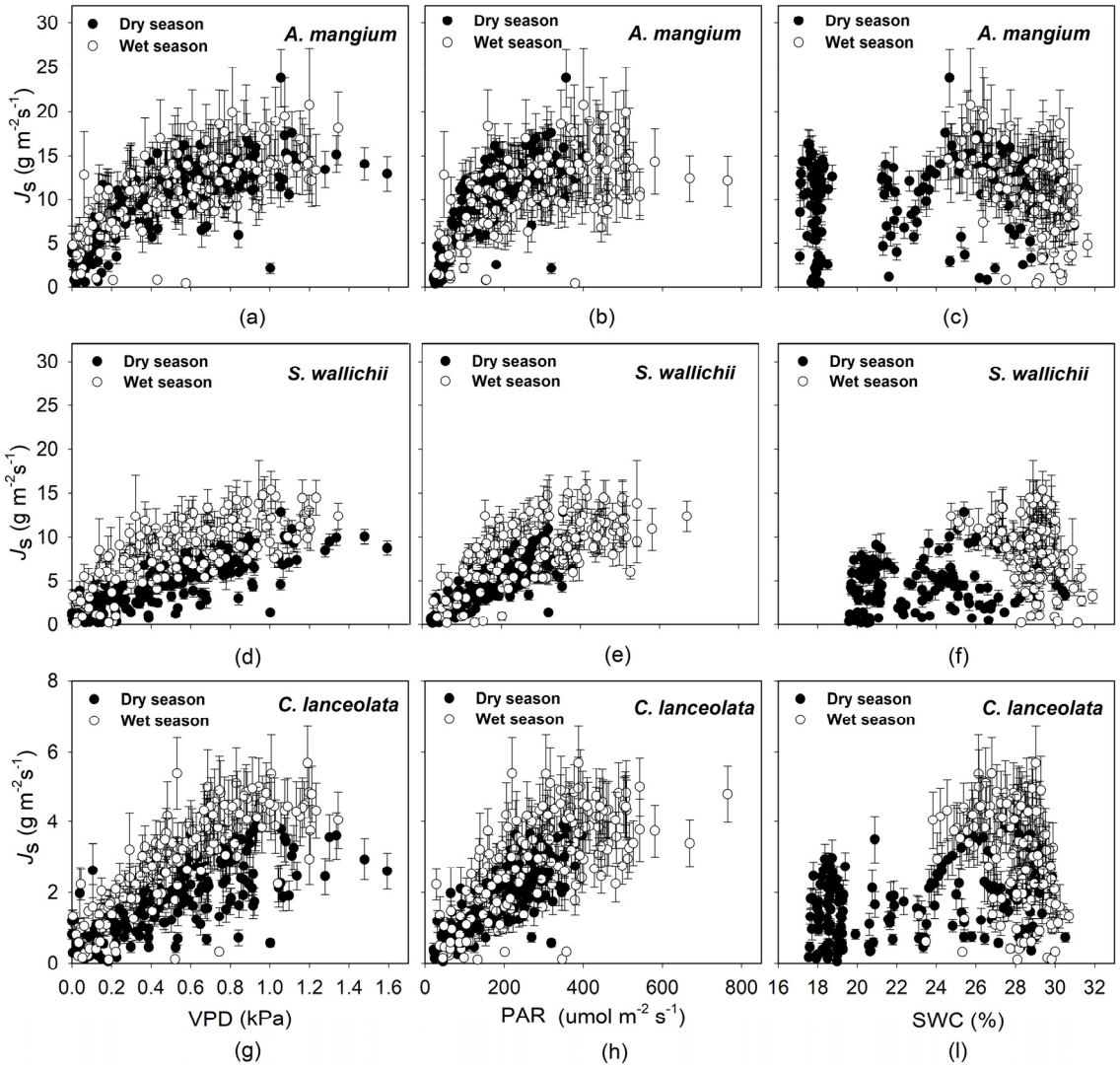

Figure 4. Raw data of daily (including daytime and nighttime) sap flux density (J_s ± standard error) to average vapor pressure deficit (VPD) at (**a**) *A. mangium* site, (**d**) *S. wallichii* site, (**g**) *C. lanceolata* site; photosynthetically active radiation (PAR) at (**b**) *A. mangium* site, (**e**) *S. wallichii* site, (**h**) *C. lanceolata* site; and soil water content (SWC) at (**c**) *A. mangium* site; (**f**) *S. wallichii* site; (**l**) *C. lanceolata* site in the dry and wet seasons. (note that the y-axis of *C. lanceolata* has a different scale compared with that of the other two species).

On the hourly scale, the results were similar to the daily scale, except for *S. wallichii* and *C. lanceolata* in dry season (see Table 4 vs. Table 5). The J_s of *S. wallichii* and *C. lanceolata* was more sensitive to VPD but less sensitive to PAR on hourly than daily scale.

For all species the correlation of the model residuals with temperature was statistically significant in the dry season and for *C. lanceolata* in the wet season as well. The strongest correlation was observed in *A. mangium* (Table 7). The effect of wind speed was also tested and no effect on J_s was found.

Table 4. Model relating daily J_s to environmental factors in different seasons and species.

Effect	***A. mangium***		***S. wallichii***		***C. lanceolata***	
Season	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**
In (J_s) = In (α) + β1 × In (*PAR*) + β2 × In (*VPD*)+ β3 × In (*SWC*)						
In (α)	−0.40A	−1.91 *a	0.27A	−4.00 *b	−1.46 *A	−4.31 *b
T-value	*−0.81*	*−5.28*	*0.40*	*−10.15*	*−3.31*	*−12.17*
β1	0.24 *A	0.70 *a	0.32 *A	1.25 *b	0.38 *A	1.00 *c
T-value	*6.30*	*14.74*	*6.93*	*25.82*	*10.40*	*21.20*
β2	0.19 *A	0.27 *a	**0.33** *B	**0.07** *b	**0.39** *B	**−0.01** b
T-value	*8.29*	*8.82*	*11.00*	*2.10*	*17.86*	*−0.37*
β3	−0.83 *A	−0.32 *a	−0.05A	0.78 *b	**−0.32**A	**0.35** *b
T-value	*−3.12*	*−3.71*	*−0.11*	*5.68*	*−1.31*	*3.87*

We compared the effects in one species between different seasons and in one season between different species based on the 95% confidence intervals (Supplementary Material Table S1). If they did not overlap, the difference was significant. The significant difference between seasons within one species is marked in bold. The significant difference between the species in one season is marked with a letter: Same letter indicates that the species behave in the same way and are not significantly different from each other. All estimates marked with an asterisk are significantly different from zero at $p < 0.05$.

Table 5. Model relating hourly J_s to environmental factors in different seasons and species.

Effect	***A. mangium***		***S. wallichii***		***C. lanceolata***	
Season	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**
In (J_s) = In (α) + β1 × In (*PAR*) + β2 × In (*VPD*)						
In (α)	−0.27A	−0.06 a	-0.28A	−1.26 *b	−0.75 *A	−1.20 *b
T-value	*−0.89*	*−5.28*	*0.40*	*−10.93*	*−4.46*	*−7.67*
β1	0.33 *A	0.37 *a	0.38 *B	0.49 *b	0.26 *C	0.29 *c
T-value	*47.20*	*58.08*	*38.86*	*57.51*	*35.11*	*39.24*
β2	0.18 *A	0.40 *a	0.42 *B	0.73 *b	0.53 *C	0.54 *c
T-value	*20.08*	*37.74*	*40.02*	*60.11*	*55.78*	*43.13*

We compared the effects in one species between different seasons and in one season between different species based on the 95% confidence intervals (Supplementary Material Table S2). If they did not overlap, the difference was significant. The significant difference between seasons within a species is marked in bold. The significant difference between the species within a season is marked with a letter: The same letter indicates that the species behave the same way and are not significantly different from each other. All estimates marked with an asterisk are significantly different from zero at $p < 0.05$.

Table 6. Model estimates relating the daily mean sap flux density (J_s) to environmental factors in different soil water content (SWC) layers.

Effect	***A. mangium***			***S. wallichii***			***C. lanceolata***		
Level	**SWC1**	**SWC2**	**SWC3**	**SWC1**	**SWC2**	**SWC3**	**SWC1**	**SWC2**	**SWC3**
In (J_s) = In (α) + β1 × In (*PAR*) + β2 × In (*VPD*) + β3 × In (*SWC*)									
In (α)	−1.81 *	−1.32 *	−1.72 *	−1.43 *	−0.74	−1.74 *	−3.04 *	−3.33 *	−2.99 *
β1	0.55 *	0.51 *	0.52 *	0.70 *	0.65 *	0.74 *	0.73 *	0.76 *	0.74 *
β2	0.26 *	0.29 *	0.29 *	0.32 *	0.34 *	0.29 *	0.26 *	0.24 *	0.25 *
β3	−0.67 *	−0.55 *	−0.71 *	0.48 *	0.85 *	0.44	0.18 *	0.11	0.28

SWC was divided into three layers: SWC1 (0–30 cm), SWC2 (31–60 cm) and SWC3 (61–150 cm). All estimates marked with an asterisk are significant at $p < 0.05$.

Table 7. Effects of temperature on the residual of the model in wet and dry seasons.

Species Effect	**Wet Season**		**Dry Season**	
	R	***p***	***R***	***p***
A. mangium	0.04	0.08	0.13	<0.0001
S. wallichii	−0.01	0.654	0.08	0.01
C. lanceolata	0.07	0.01	0.09	<0.0001

4. Discussion

We found that both native species (*S. wallichii* and *C. lanceolata*) differed clearly in their stomatal sensitivity (at the daily scale) from one season to another, while the exotic *A. mangium* did not (Table 4). In the dry season, the parameter β2 of both native species was close to zero (Table 4). This means tight stomatal control, i.e., high sensitivity of g to VPD in *S. wallichii* and *C. lanceolate*. Earlier studies had also shown a sensitive canopy stomatal regulation in some tropical trees, resulting in partial canopy stomatal closure at VPD >1 kPa [35]. This implies that tropical trees had a conservative water use strategy when exposed to short-term drought [36,37]. High sensitivity of canopy stomatal control to VPD has been linked to conditions of water stress [38,39]. This result could be explained by consequent drought stress in *S. wallichii* and *C. lanceolata* during the dry season. For these two species, the positive correlation between J_s and SWC indicates that water availability was limiting their water use in the dry season (Table 4). In contrast, the difference of stomatal behavior between the wet and dry seasons was not clear for *A. mangium* (Table 4). This may be because increasing SWC had a negative effect on the J_s of *A. mangium* during both seasons (Table 4). One possible reason for this could be that *A. mangium* was suffering from too high soil water content. During the wet season, the J_s of two native species was more sensitive to VPD than that of *A. mangium* (Table 4), indicating that *A. mangium* was more sensitive in canopy stomatal control to VPD than the native species were.

On the hourly scale, the dynamics of actual transpiration rate, which responds quickly to changes in environmental conditions, might be considerably different from those of the sap flow rate due to the time lag between these two variables [40,41]. The response of J_s to the environmental conditions were similar to the daily scale when analyzed on the hourly scale, except in the case of *S. wallichii* and *C. lanceolata* in dry season (see Table 4 vs. Table 5). The canopy conductance per sapwood area response of these species was much stronger in daily than in hourly scale during the dry season. One reason for this difference in behavior could be the role of internal water stores within the tree and the decoupling of transpiration rate from the sap flow rate [42]. *S. wallichii* and *C. lanceolata* seemed to be suffering from drought stress during dry season (Table 4), and diurnal usage and refilling of internal water stores maybe a strategy under drought condition [43]. It is also known that the role of internal water stores increases when the total water usage is low [44,45], and the lowest water usage occurred in *S. wallichii* and *C. lanceolata* in the dry season (see the intercept, parameter in (α), in Table 4).

The J_s of *S. wallichii* and *C. lanceolata* was very sensitive to PAR during the dry season, even more sensitive than that of *A. mangium* (Table 4). Liu et al. (2014) [46] found the same result i.e., that the J_s of *C. lanceolata* was more sensitive to PAR than VPD during the dry season in Eastern China. A possible explanation for this could be the lower light levels during the dry season in winter as the light-response curve of photosynthesis is steeper at low light levels [47]. The greater sensitivity of the J_s of *C. lanceolata* to light during the dry season may also be linked to their suffering from drought stress, as drought stress has been found to increase the sensitivity of canopy stomatal control to light [48].

Increasing SWC had a negative effect on the J_s of *A. mangium* during both seasons (Table 4), suggesting that soil water content could have been too high for *A. mangium*. The J_s was similar between the dry and wet seasons for *A. mangium* (Figure 3). One would expect the J_s to be higher during the wet season because of the higher level of light. However, this was not the case and could be due to too much water in the soil in the wet season causing oxygen deficiency and preventing optimal root functioning [49]. It has been reported that *A. mangium* is intolerant of excessively wet soil and grows better on sites with good drainage [50]. We also found that J_s of *A. mangium* was sensitive to temperature. This finding corresponds to the report of Booth and Hong (1991) [11] that low temperatures in winter reduce the growth of *A. mangium* in Guangzhou (Guangdong Province). The effect of SWC on J_s was significantly positive for *S. wallichii* and *C. lanceolata* only during the dry season. For *C. lanceolata* in eastern China, Liu et al. (2014) [46] also found that SWC (at depths 5, 10, 15 and 40 cm) had positive effect on J_s in winter (dry season).

We also analyzed the effect of SWC at different soil depths on J_s (Table 6), because SWC at different layers makes a different contribution to plant water use due to a variety of root system depths for

different tree species [51]. The J_s of *A. mangium* was sensitive to SWC in all layers, but the native species (*S. wallichii* and *C. lanceolata*) were not sensitive to SWC in deeper soil layers (Table 6). This indicates that *A. mangium* may have deeper roots than both native species and could extract water down to at least 0–150 cm depth. Although Pan et al. (1996) [52] described that the roots of *A. mangium* were shallow (most roots concentrated in the upper 28cm), several other authors' reports support our results. For example, the rooting depth of *A. mangium* has been observed to be deeper than 1 m [53] and the fine roots to reach down to 12 m in monospecific stands of *A. mangium* [54]. Fine roots of *C. lanceolata* trees have been reported to be mainly distributed in the 0–20 cm soil layer in subtropical China [55], which is consistent with that *C. lanceolata* may only extract water from the soil layer at 0–30 cm depth (Table 6), while *S. wallichii* seemed to use water from 30–60 cm depth (Table 6). Also, Zeng (1988) [56] reported that most of the roots of *S. wallichii* in south China were concentrated in the 30–50 cm soil layer. Such differences in rooting depth may also explain why J_s was reduced in *S. wallichii*, and *C. lanceolata* but not in *A. mangium* (Figure 3) during dry season when soil water availability was low. *A. mangium* is likely the most deeply rooted among the three species studied, and therefore had the least response to dry season [57].

The mean daily maximum J_s of *A. mangium* at 9–55 g $m^{-2}s^{-1}$ was lower than the values reported for *A. mangium* at Sardinilla, Panama (81 g $m^{-2}s^{-1}$) of larger mean DBH [58], but similar to the values measured in an *A. mangium* plantation in South China (11–80 g $m^{-2}s^{-1}$) of similar DBH [12]. The maximum J_s of *S. wallichii* was 17 g $m^{-2}s^{-1}$ in DBH = 15.5 cm trees in the Lesser Himalayas of Central Nepal [59], which was similar to the daily maximum J_s of *S. wallichii* (11–24 g $m^{-2}s^{-1}$) in the same DBH at our site. The J_s of *C. lanceolata* was much smaller than that of the two other species, and its peak value was less than half that of the other species (Table 3). The reason for the low J_s of *C. lanceolata* might be that *C. lanceolata* is a coniferous species, which generally uses less water in relation to broad-leaved trees [60]. Moreover, the canopy stomatal conductance has been found to be lower in *C. lanceolata* than in broad-leaved trees, which also leads to lower J_s in *C. lanceolata* stems [61]. This could also be explained by the thick wax layer on the leaf surface of *C. lanceolata* [61]. Although Zhang et al. (2016) [62] found a similar J_s of *C. lanceolata* with similar DBH to our results in Southwest China, the J_s of *C. lanceolata* was much smaller than reported for other locations in southern China [61,63]. Moreover, Li and Ritchie (1999) [64] reported that *C. lanceolata* requires well-drained soil and that it will not grow well in wet conditions. Jøker (2000) [65] also found that the best growth of *C. lanceolata* is obtained on well-drained loamy soils. According to Li and Ritchie (1999) [64], there are only a few places in South China which offer suitable terrain for *C. lanceolata* to grow well. Our results of mean daily maximum J_s in the range 9–55 g $m^{-2}s^{-1}$ for the *A. mangium* site and 11–39 g $m^{-2}s^{-1}$ for the *S. wallichii* site both fall within the lower range of 4–139 g $m^{-2}s^{-1}$ reported for subtropical and tropical tree species [58,60,66]. Low J_s was the result of continuously high air humidity at the study site (Figure 1e), with VPD rarely exceeding 1 kPa (Figure 1d), which was supported by earlier studies on different species in the same area [67] and on a perhumid tropical forest of Sulawesi, Indonesia [68].

The annual rainfall (1600+ mm/year) of the observation site is enough to keep SWC at over 20% even in the cool-dry season, which might not induce severe evapotranspiration depression for any of the species at present. However, long-term observations have shown that droughts are becoming frequent and more severe, leading to declining SWC in the extended dry season [24]. Hu et al. (2018) [26] also showed that the dry season extended from November–March during the 1964–1983 period to October–April during the 2001–2010 period in the Heshan area (our sites), and they found that the extended dry season reduced transpiration in *Schima superba* (the same family as *S. wallichii*). Based on our results, we speculate that the exotic species *A. mangium*, which prefers higher temperatures and drier soil, will become more suitable in Southern China, whereas the more drought-sensitive native species *S. wallichii* and *C. lanceolata* could suffer more severely from water stress under future meteorological and soil conditions.

5. Conclusions

We found distinct differences in how PAR, VPD and SWC controlled the water use of the three plantation species. *S. wallichii* and *C. lanceolata* differed clearly in their stomatal behavior and J_s at the daily scale from one season to another, while *A. mangium* did not. *S. wallichii* and *C. lanceolata* may suffer from water stress in dry season, but for *A. mangium* there seemed to be even an excess amount of water in the soil in both seasons. Extended dry season in the research area will likely impact the ecosystem hydrologic cycle and thus the water use of the studied species in the future.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/11/2/206/s1, Table S1: 95% confident interval of model relating daily sap flow density (J_s) to environmental factors in different seasons and species. Table S2: 95% confident interval of model relating hourly sap flow density (J_s) to environmental factors in different seasons and species.

Author Contributions: Conceptualization, Q.W. and T.H.; data curation, Q.W.; formal analysis, Q.W., A.L., and Y.S.; funding acquisition, P.Z. and G.N.; investigation, Q.W., X.C., L.O., L.Z., G.N., D.S., and X.R.; methodology, Q.W. and A.L.; project administration, P.Z.; resources, W.S.; supervision, P.Z.; visualization, Q.W. and T.H.; writing—original draft, Q.W.; writing—review and editing, A.L., P.Z., and T.H. All authors have read and agreed to the published version of the manuscript.

Funding: This study was financially supported by the National Natural Science Foundation of China (Grant Nos. 41630752, 31670410), the National Key Research and Development Programme (2016YFC0500106-02) and Guangzhou Science and Technology Project (201707010226).

Acknowledgments: We thank Xiuhua Zhao, Yaxing Zhang, Zhipeng Chen and Xiaoming Zeng for their assistance with the field works and Heshan Station for providing us with meteorological data in 2017. We also thank Cathryn Primrose-Mathisen for checking the language of the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

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